Simulating Aerial Migrations through Use of Empirical Movement Models

Honors Undergraduate Research Thesis

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Abstract

Aerial migrations are historically difficult to observe and quantify, especially the environment in which these migration take place. However, with increasingly accurate tracking methods and international datasets containing remote sensing and weather renalyses, it is becoming easier to observe this environment and find the conditions that mostly affect the migrants. Track annotation is the method of combining the tracking data with the environmental data, and can be used to create models of the animals' movement. I performed a track annotation of Swainson's thrush and created an empirical model based on the environmental conditions that mostly affect the flight. A Swainson's thrush (*Catharus ustulatus*) is a small songbird that migrates from northeastern North America to Central and South America in the winter. This annual migration involves a 1000-kilometer trip across the Gulf of Mexico. Little is known about the details surrounding this annual flight, including the variables that affect the flight itself. In a National Science Foundation (NSF) funded experiment, the thrushes are tracked by a radio transmitter which allows us to record arrival and departure timestamps of the transGulf flight. The Environmental-Data Automated Track Annotation (Env-DATA) system—a data exploration system developed through Movebank (www.movebank.org) and The Ohio State University allows us to link the movement track with data from global and regional weather reanalysis models and remote sensing. I annotated the movement tracks with several different environmental variables and followed a hierarchal process to build a series of empirical movement models. I concluded that the combination of boundary layer height and wind speed most strongly affect the flight.

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Introduction

Movement ecology is a historically difficult subject to research due to the wide spatial and temporal extent of migrations and the remoteness of migratory environments [Bowlin et al., 2010]. Aerial migrations add another challenge to the subject due to the complex role that atmospheric conditions play in the movement. Furthermore, with any predictive movement model, it is difficult to determine which of the interdependent environmental variables is most probably affecting the migration pattern [Dodge et al., 2014]. However, as GPS technology has developed, collecting this migration data has gotten easier, and with emerging track annotation tools such as movebank Env-DATA (Environmental-Data Automated Track Annotation), analyzing that data is getting easier as well. Env-DATA is an application of Movebank (www.movebank.org) that allows the user to automatically annotate movement tracks with atmospheric and landscape conditions [*Dodge et al., 2013*]. It is important to analyze these migrations that we have recorded because they give us insight into the lives of the birds that make the migrations. One such way to analyze annotated movement track data is to use empirical modelling to determine the environmental controls on animal movement. The track-annotation approach [Mandel et al., 2011] allows linking data from gridded remote sensing and model-reanalyses to the reported movement locations as a surrogate for direct environmental observations in route.

I analyzed flight data from Swainson's thrushes (*Catharus ustulatus*), and built a series of empirical models to determine the environmental conditions that affect flight speed the most. In a National Science Foundation (NSF) funded project, the thrushes are tracked by a radio transmitter which allows us to record timestamps when the birds depart Fort Morgan Peninsula, Alabama and arrive in the Yucatan Peninsula, Mexico. I combined the location data collected from the studies with meteorological data from global reanalysis datasets, such as those run by the European Centre for Medium-Range Weather Forecasts (ECMWF), and from direct observation datasets, such as NASA's Tropical Rainfall Measuring Mission (TRMM). This data is collected and recorded at regular intervals (usually 3 or 6 hours) every day and can be used to determine the weather conditions during the migration of the birds. By using the track annotations and reducing the movement of the birds to flight speed, I created an empirical model that describes the environmental factors that most strongly affect the flights of the species.

I hypothesized that the flight speed will be largely dependent on environmental conditions. The thrushes have a long flight across the Gulf of Mexico without stopping, which makes it likely that the environmental conditions will largely affect the speed of the flight. When analyzing migration data, it is important to consider the movement ecology paradigm, which calls for the use of both internal and external factors to be considered when predicting the consequences of movement [*Nathan et al., 2008*]. Under this paradigm, environmental variables will directly affect the capacity to move by governing the energetic cost of moving [*Dodge et al., 2014*]. For the thrushes, certain environmental conditions will require larger energy expenditure to keep up a certain speed.

Methods

Study Species

A Swainson's thrush (*Catharus ustulatus*) is a small neartctic-neotropical songbird species that breeds in Canada and migrates to Central and South America in the winter. There are two major populations of Swainson's thrushes: the coastal population and the continental population. The coastal population migrates down the pacific coast to Mexico or Costa Rica and the continental population migrates along an eastern route to Panama and South America. The migration of the continental population involves a long flight without stopover sites across the Gulf of Mexico. This transGulf migration takes an average of about 22 hours and often occurs overnight. The nature of this migration makes tracking and observing these birds difficult. The birds generally weigh between 23 and 45 grams, so any tracking device attached to the birds must be lightweight and not affect the migration path. GPS transmitters are larger than this size limit. This poses a strong limitation of the technology used for tracking these, and similarly sized, small birds. Radio telemetry provides the opportunity to locate the birds using a very small radio transmitter. The observation, however, is limited to the locations of the telemetry antennas, and typically these types of observations provide very sparse information of the movement track.

Figure 1 Swainson's thrush with radio-transmitter attached to back. Photo credit: William Cochran

Study Area/Data Collection

I studied the Swainson's thrush population that migrates from the Bon Secour National Wildlife Refuge on the Fort Morgan Peninsula in Alabama (USA) to the Ría Lagartos Biosphere Reserve located along the northern coast of the Yucatan Peninsula in Mexico (21°31′N, 87°40″W) in the fall. The birds were tracked using radio-telemetry technology. This technology allows for tracking via a transmitter. The idea is that there is a tower equipped with a receiving unit and a transmitter attached to the bird you wish to track. The transmitter has a specific frequency that is picked up by the receiver once the bird is close enough. Once the receiver picks up on the frequency, it records the date and time of contact. The birds were captured using mist nets while flying through the wildlife refuge in Alabama. After capture, the birds were weighed, measured, and fitter with radio-transmitters with a frequency of 164.523 hertz. These transmitters are glued to the back of the birds. This glue often wears off in several days. This method allows the data to be collected automatically without having to recapture the birds in Mexico to recover the transmitter. The study area included 10 radio-telemetry towers (Figure 2), 3 in the Fort Morgan Peninsula in Alabama and 7 in the Yucatan Peninsula. Each tower had an Automated Receiving Unit (ARU, Sparrow systems, Inc.) attached to six antennas. The towers in

Alabama recorded when the birds were departing on their flight across the Gulf of Mexico as well as the flight direction. The towers on the Yucatan each consisted of an ARU with two antennas and recorded when the birds arrived on the continent after the flight across the Gulf of Mexico. The Yucatan towers were located in Sisal, Chicxulub, Dzilam de Bravo, Rio Lagartos Field Station, El Cuyo Field Station, Holbox, and Isla Contoy, creating a "fence" of recievers. There were 145 birds tagged from September 26, 2009 to October 21, 2014, however, only 23 birds were recorded crossing in range of the telemetry towers in the Yucatan within a reasonable time. Of these 24 birds, six were documented in 2009, eight in 2010, four in 2012, two in 2013, and three in 2014. It is likely that the birds that were not recorded in the Yucatan either took another route to their destination or did not survive the crossing. Of these 23 birds, the minimum flight time was 14.85 hours, the maximum was 34.55 hours, and the average was 21.77 hours. In order to build my model, I used a sample area of 757,687,366 square kilometers, between longitudes 91 °W and 85 °W and between latitudes 31 °N and 20 °N (shown in figure 3). This area encompassed all of the telemetry towers and the area over which the birds were flying.

Figure 2 Radio-telemetry tower in Alabama
Photo Credit: Jaci Smolinsky

Movebank and Env-DATA

Movebank is an online database of animal tracking data, which provides users with a place to store, manage, analyze, and share animal movement data [*Kranstauber et al., 2011*]. The Env-DATA system is an extension of movebank that automatically annotates tracks with environmental data [*Dodge et al., 2013*]. The annotation data can be easily read into other software programs such as MATLAB, R, and Google Earth. Environmental data is available from many international datasets including NASA's MODIS products, NCEP Global and North American Regional Reanalyses (NARR), the European Centre for Medium-Range Weather Forecasts (ECMWF), Oregon State University Ocean Net Primary Production, NOAA's Ocean Surface Current Analyses (OSCAR), and NASA's Tropical Rainfall Measuring Mission (TRMM).

In addition to the data collected from the various datasets, Env-DATA can also annotate tracks with derived variables such as wind support and uplift [*Dodge et al., 2013*]. There are two types of annotations available through Env-DATA: (1) a gridded geographical area or (2) a set trajectory. A gridded annotation provides the user with environmental data for a set geographical area, while the trajectory annotation provides the user with data covering only the locations included in the track data [*Dodge et al., 2013*]. The thrush data only contained two locations for each bird, a departure and an arrival, so I used the gridded area annotation method to get an estimate of the environmental conditions the birds would experience during the flight. This gridded area is illustrated in figure 3.

Annotation Variables

Remote-Sensing data and data from global weather reanalyses were used to generate information about specific environmental conditions during the flight. Weather reanalysis datasets are the products of atmospheric models that are forced with a large number of satellite, meteorological stations, and weather balloon observations. The advantage of using these to traditional direct weather observations is the regular resolution across the whole dataset as well as the predictable error rates [*Mandel et al., 2011*]. I used two different reanalyses to annotate the thrush flight: the European Centre for Medium-Range Weather Forecasts (ECMWF) ERA-Interim Reanalysis dataset and the NCEP North American Regional Reanalysis (NARR). The ECMWF dataset has a spatial granularity of 0.75 degrees and a temporal granularity of 3-hourly [*Dee et al., 2011*]. The spatial resolution of the NARR dataset was 32 x 32 kilometers at 3-hourly temporal resolution [*Mesinger et al., 2006*]. Additionally, I retrieved data from NASA's Tropical Rainfall Measuring Mission (TRMM) that has a spatial resolution of 0.25 degrees and a temporal resolution of 3-hourly [*Kummerow et al., 1998*]. I annotated the study area with five different variables: (1) wind speed (2) temperature (3) humidity (4) height of the planetary boundary layer (5) precipitation. These variables are the major environmental factors that could potentially affect the birds during their flights.

The wind speed data, as U (East-West) and V (North-South) components at ten meters above sea level, air temperature 2 meters above sea level, and atmospheric water content (humidity) were all retrieved from the ECMWF reanalysis dataset. I chose to use the surface values of wind speed, temperature and humidity because the birds' altitude is unknown throughout the flight. However, these variables tend to be correlated throughout the atmospheric column, so the surface values are an acceptable estimate for the values at the height at which the bird is flying. The height of the boundary layer (HPBL) data was retrieved from the NARR dataset. The NARR model combines the NCEP Eta Model and the Regional Data Assimilation System (RDAS) to obtain the data. Finally, the precipitation data was obtained from the precipitation data from the TRMM dataset as combined precipitation. TRMM is a joint mission between the US and Japan to monitor tropical rainfall. The data is retrieved via a satellite and uses the 3B42 algorithm to combine several different precipitation readings and produce the merged-infrared precipitation rate in millimeters per hour (mm/hr) [*Kummerow et al., 1998*].

The data for the wind speed components was used to calculate three major wind characteristics: (1) wind speed, (2) wind direction, and (3) wind support. These calculations were completed using equations published by *Dodge et al.* [*2013*]. These were defined as:

(1) $$w_s = \sqrt{U + V^2}$$

(2) $$w_d = \tan^{-1}(U, V) \times \left({}^{180}/_{\pi}\right)$$

(3) $$w_p = w_s \times \cos(w_d - h_d)$$

where U and V are the wind components in meters per second, w_s is the wind speed in meters per second, w_d is the wind direction in degrees, w_p is the wind support in meters per second, and h_d is the bird's movement heading in degrees.

All of these variables were interpolated over the aforementioned gridded area (see figure 3) with a resolution of 25 x 25 kilometers. This resolution was chosen to provide fine uniform coverage across all of the datasets, which had varying spatial resolutions. Additionally, each variable was annotated in time for specified timestamps that started on departure date and time, increased by a set amount (depending on the temporal distribution of the dataset), and ended on the arrival date and time. I used all of my annotation data to build several different individual based regressions models to predict the environmental parameters that affect the bird migration for each species.

Migration Models

Due to the nature of the data collection method, there were only two points per bird—the departure and arrival times and locations. In order to deal with the little amount of data, I assumed a straight flight path between the departure and arrival locations (Figure 3). This would have been the least amount of distance and potentially use the least amount of energy, so I am confident that it is somewhat close to the actual path taken by the birds. This assumption allowed me to determine an estimate of the flight speed of the birds and build a model to determine the environmental factors that affect that flight speed.

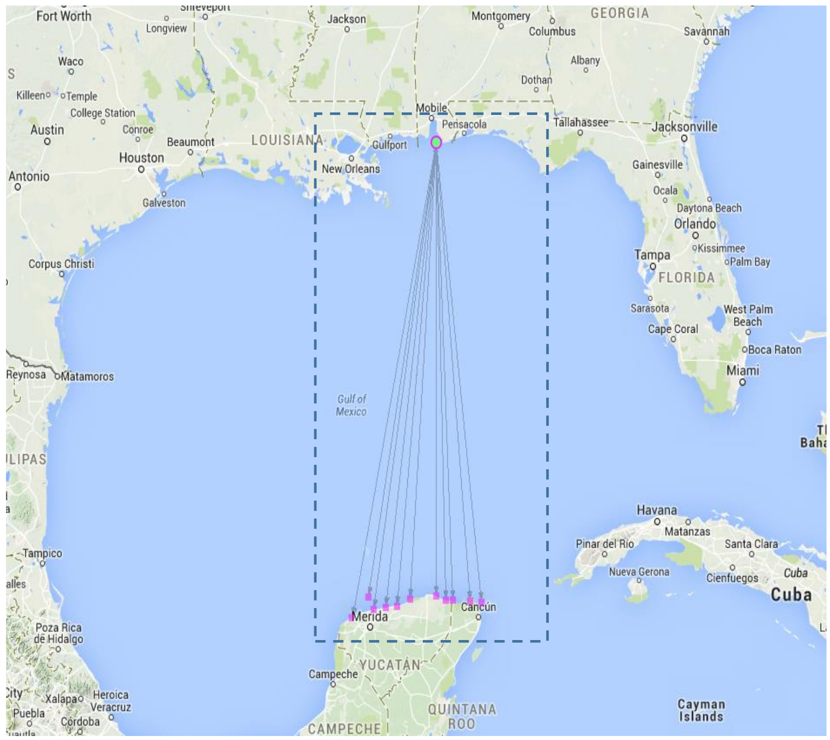

Figure 3 Assumed tracks of Swainson's Thrushes recorded in the Yucatan Peninsula from Movebank.org. The dashed box illustrates the area that was annotated with the environmental data.

Furthermore, due to the large amount of environmental data retrieved from the gridded analysis, I took the average for all locations over each time-step per bird. I then took a regional mean over the entirety of the Gulf-crossing for each bird. This allowed me to get a single point for each bird to represent the average environmental conditions experienced during the flight.

I used this data to test pair-wise correlations between each environmental variable and the flight speed. I then discarded the variables that did not have a significant effect. Using the variables that were significantly correlated and following a step-wise hierarchal method, I built a set of increasingly complex empirical models using the aforementioned variables as parameters for each species. For each new model, a comparison of the goodness of the fit and the information criterion was used to determine if the model was a justified description of the environmental conditions that would affect the migration. If the information criterion proved that the model was less justified, then I moved on to the next potential model. Process such as this have been use to create predictive movement models for many different animals [e.g., *Bartlam-*

Brooks et al., 2010; Bohrer et al., 2014]. Through this process I was able to determine the parameters that would affect the flights the most.

In all models, I used the regression function, *regress*, in MATLAB.2014a software to determine the fit (R^2) of the model. I used the Akaike information criterion with a correction for sample size (AICc) to reconcile the goodness of the fit with the number of parameters used in the model to determine the most justified model [*Akaike 1974*]. I also used the forward stepwise analysis in JMP.11 software to calculate the model statistics, including the AICc.

Results

The boundary layer height (HPBL) was the variable most strongly correlated with the flight speed of the birds (Table 1). As the height of the boundary layer increases the birds tend to fly faster, as shown in Fig. 4b. In addition to the boundary layer height, the wind speed was also significantly correlated with flight speed (Table 1). The wind speed was calculated by using the U and V components of the wind found in the ECMRWF dataset, without taking flight direction into account. The flight speed of the bird increases as the wind speed increases, shown in Figures 4a. Finally, both humidity and temperature were also correlated flight speed (Table 1). In both cases, the flight speed decreases as the temperature and humidity increase, shown in Figures 4c and 4d. I also tested the correlation between flight speed and precipitation, as well as between flight speed and wind support, however, neither of the models were statistically significant, these can be seen in Table 1.

Table 1 Summary of correlation data (coefficient of determination [R^2] and significance [P value]) between listed variables and the flight speed of the thrushes. Relationships were considered to be not significant (NS) when the P value (P) was greater than 0.05. These variables were removed from later models.

Model	R^2	P
HPBL	0.4676	< .001
Wind Speed	0.4574	< .001
Temperature	0.3526	0.0028
Humidity	0.2227	0.0230
Precipitation		NS
Wind Support		NS

Starting with the single variable models seen in Table 1, I created a series of hierarchal models with multiple variables. The conceptual path I followed can be seen in Figure 6. With each hierarchal level I added a new statistically significant variable to the model. I found the R^2 value for each new model to test the goodness of the fit, which should increase with each new variable. However, adding more variables adds more complexity to the model and decreases the probability of it happening in the environment, so I also found the AICc for each new model. The AICc is an information criterion that gives one an idea of how likely the model is—if the AICc is closer to zero than the previous model (convergence), the new model stands. My final model included HPBL and wind speed.

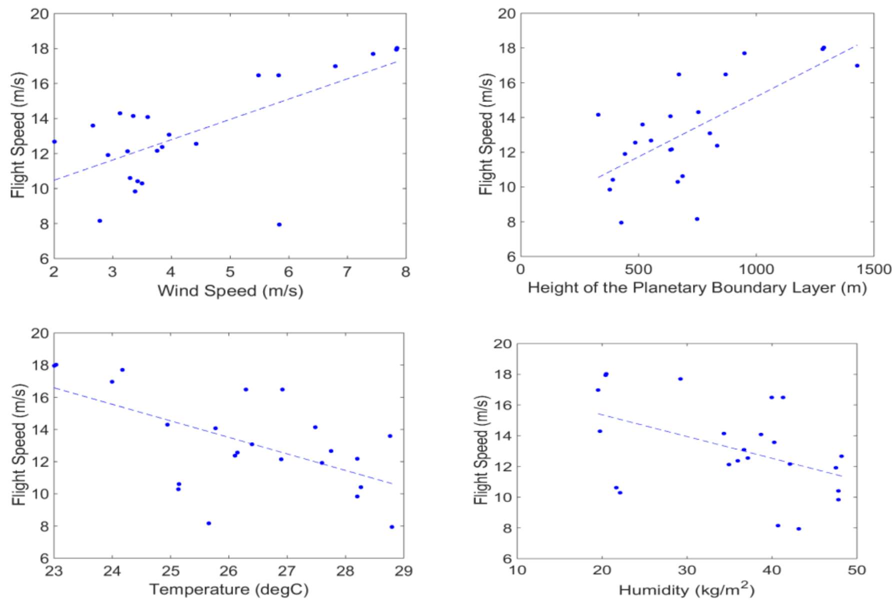

Figure 4 Correlations between thrush flight speed and (a) wind speed, (b) height of the planetary boundary layer, (c) temperature, and (d) Humidity.

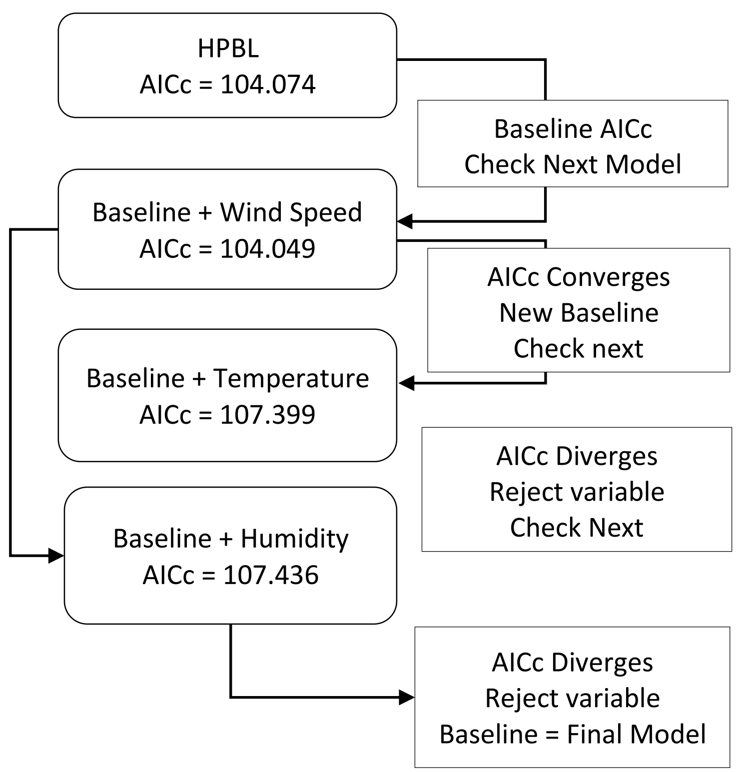

Figure 5 The conceptual work flow to construct the empirical model for thrush's Gulf-crossing speed

Discussion

The final model was boundary layer height plus wind speed, this means that the transGulf migration of the Swainson's thrushes is mostly affected by the boundary layer height and the wind speed. As shown in figure 4b, the flight speed increases with increasing boundary layer height. The planetary boundary layer is the atmospheric layer that is directly influenced by the planetary surface. In this layer, many meteorological attributes experience rapid fluctuations. The height of this layer experiences changes that are largely based on the surface temperature of the ocean [*von Englen and Teixiera, 2013*]. An ocean that is warmer than the atmosphere creates a heat flux that drives thermal uplift and increases the high of the boundary layer. Conditions such as these would be beneficial to the thrushes as they fly across the Gulf of Mexico. Although the thrushes aren't soaring birds the thermals could still help them conserve energy by gliding through the buoyant eddies instead of flapping their wings. Also shown in figure 4a, as the wind speed increases, the flight speed also increases. The wind during the time of flight was moving in the southwest direction, so it is reasonable to assume that as the speed increased the bird would be able to fly downwind at a faster pace. Swainson's thrushes are fairly small birds, so it is likely that they fly with the wind to conserve energy. This means that the ideal flight pattern would be a higher boundary layer height and moderately high wind speeds.

That being said, there are other conditions that could potentially affect the flight—such as temperature or humidity. These other factors, however, were found to not add anything substantial to the model. Although the addition of variables increased the goodness of the fit, it also increased the complexity of the model, and in the case of the variables not included in the model, the increase in fit goodness did not outweigh the increased complexity. This determination of what variables add or do not add useful information to the model was done using the Akaike Information Criterion with a correction of sample size (AICc) [*Akaike 1974*]. The AICc is a method of evaluation that takes into account the increase in the goodness of the fit and the increase in complexity and determines whether the information gleamed from adding a new variable was useful. In the case of variables such as temperature or humidity for the thrushes, the value in the added variable was likely dependent on a previously added variable, so there was not enough new information to rationalize the increase in complexity.

As with many models, there are limitations to the method I used to determine the factors in my final model. One such limitation was the assumption that I made about the flight path. The method used to track the thrushes allowed for only two recorded timestamps—departure from Alabama and arrival in Mexico, everything in between these points is unknown. I assumed a direct flight path, which would be the quickest thus using the least amount of energy (theoretically). The flight across the Gulf is a long, dark flight with no landmarks, it would be easy for a bird to get blown off course and reach land at a different point than the Yucatan Peninsula. However, there were 23 thrushes that reached the Yucatan Peninsula in a reasonable amount of time (less than 35 hours). It is safe to assume that these thrushes flew in a relatively direct path.

Had there been more data detailing the birds' locations during the flight, I would have been able to obtain a more accurate estimate of the conditions the birds faced during their flight. However, the birds are too small to be fitted with a GPS tracker, so finding a way to work with the limited amount of data was necessary. To do this I annotated an entire grid of location points during the entire flight of the bird and averaged those values over every point and every timestamp to get a single value for duration of that bird's migration. The area that I annotated was relatively small and the times relatively short, so most of the data within each grid was similar. Therefore, the averaged values were fairly accurate and their use in my model justified.

Finally, my models did not take biological factors, such as age, sex, or the amount of fat on the body, into account. These factors could affect the flight speed of the bird in many ways, perhaps the younger birds fly slower because they are new to the migration, or the fat birds fly slower because they are heavier. These are questions that could be answered using a similar model to my own, but with more categories and a larger sample size. I judged the sample size of both species to be so small that there was not enough variance in the biological factors to complete the analysis.

There are a few drawbacks to this method, but the tools and methods developed can be used for many different applications, and additions can be made to the model to increase accuracy and account for more factors. These models and their expansions will help the scientific community to increase its knowledge and understanding of these migratory birds.

The method I used to build my models is the foundation for movement models, and there are many expansions that can be made upon that method to increase accuracy and function. One such expansion is to include a Brownian Bridge. A Brownian bridge is a movement model that predicts the probable location of the bird based on the starting and ending locations, the elapsed time between those points, and the speed of movement [*Horne et al., 2007*]. This would eliminate the need to assume a direct flight path and would yield a more accurate model. Another expansion is to include biological factors, like I mentioned earlier. In order to do these categorical analyses, you would have to use statistical software that could account for non-numerical values, but they could answer questions like those that I posed earlier. It is important to be wary of added complexity when adding more variables like the biological ones. Finally, it would be possible to use the model to predict movement, and then go out into the field to check to see if the model was correct. For example, if you knew the average wind speed and HPBL during a single migration, you could potentially predict when the bird was going to arrive in the Yucatan Peninsula. Then once the bird did arrive, you could see if your model was accurate in predicting the flight speed.

Conclusion

Track annotation is a tool that can help us understand movement ecology more fully. There are several advantages to annotating animal tracks with environmental data. One advantage is that it is a way to analyze data that previously has not been analyzed. This analysis can shed light on patterns that were not visible at first glance. When tracking birds, the environmental variables are often not known, and if they are, they are not recorded. However, when you annotate the tracks with environmental variables, such as wind speed, HPBL, or humidity, a pattern could emerge that provides new information about what affects aerofauna during migrations. Annotating tracks with environmental data can also help to approximate atmospheric conditions that are not typically observed, such as tail wind or uplift. These environmental conditions are important to many species of birds, and can be calculated and mapped spatially and temporally using track annotations.

My model that predicts the environmental conditions that largely affect the flight speed of Swainson’s thrushes will hopefully help to increase the knowledge about migrations of songbirds and other aerial migrants. An increased understanding of these migrations will be increasingly important as our planet continues to warm and the climate continues to change. A change in climate will likely affect weather patterns in the areas that these birds migrate, which could in turn affect the migrations of birds flying over it. The greater our understanding of these migrations, the more likely we are going to prepared if something drastic does change in the migration of these birds. In addition to increasing our understanding of the migrations, increased knowledge of the factors that affect the flights of the birds can give us insight into the rest of their lives. This model can also serve as a framework for other similar models for other migratory birds or models that test other factors. This data has numerous applications, each working to increase the general understanding of aerial migrants and the factors that affect them.

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